

Solutions of Fisher and Burgers' equations with finite transport memory

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The Fisher and Burgers' equations with finite memory transport, describing reaction-diffusion and convection-diffusion processes, respectively have recently attracted a lot of attention in the context of chemical kinetics, mathematical biology and turbulence. We show here that they admit exact solutions. While the speed of the traveling wavefront is dependent on the relaxation time in Fisher equation, memory effects significantly smoothen out the shock wave nature of Burgers' solution, without making any influence on the corresponding wave speed. We numerically analyze the ansatz for the exact solution and show that for the reaction-diffusion system the strength of the reaction term must be moderate enough not to exceed a critical limit to allow travelling wave solution to exist for appreciable finite memory effect.

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Introduction: A number of nonlinear phenomena in physical [1], chemical [2] and biological processes [3, 4] are described by the interplay of reaction and diffusion or by the interaction between convection and diffusion. The well-known partial differential equations which govern a wide variety of them are Fisher [5] and Burgers' [6] equations, respectively. While the Fisher equation describes the dynamics of a field variable subject to spatial diffusion and logistic growth, Burgers' equation provides the simplest nonlinear model for turbulence. Since spatial diffusion is common to all these processes, Fick's law forms the key element in the description of transport. This description however, gets significantly modified when the memory effects are taken into account, i.e., when the dispersal of the particles are not mutually independent. This implies that the correlation between the successive movement of the diffusing particles may be understood as a delay in the flux for a given concentration gradient. Over the last several years the analysis of memory effects in diffusive processes have attracted a lot of attention [7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23] in chemical kinetics, mathematical biology and allied areas. The focal theme lies in the interesting traveling wave front solutions which have been studied extensively by several authors under various approximations. The object of the present paper is to show that the Fisher equation and the Burgers' equation with finite memory transport admit exact solutions. We numerically clarify the nature of the ansatz wherever necessary and analyze the physical implications of the solutions modified by relaxation effects and the related issues.

Fisher and Burgers' equations with finite memory transport: The starting point of our analysis is the Cattaneo's modification [24] of Fick's law in the form:

$$J(x, t + \tau) = -D \frac{\partial u(x, t)}{\partial x} \quad (1)$$

which takes care of adjustment of a concentration gradient at time t with a flux $J(x, t + \tau)$ at a later time $(t + \tau)$, τ being the delay time of the particles in adopting one definite direction of propagation. Here $u(x, t)$ denotes the field variable and D is the diffusion coefficient of the particles.

The population balance equation for the particles on the other hand takes into account of the conservation equation supplemented by a source function $kf(u)$ for the particles in the form

$$\frac{\partial u(x, t)}{\partial t} = -\frac{\partial J}{\partial x} + kf(u) \quad (2)$$

The Fisher source function $f(u) = u(1 - u/K)$ has been the subject wide interest in various context. Here the first term in $f(u)$ signifies the linear growth followed by a nonlinear decay due to the second one; k and K being the growth rate constant of the population and carrying capacity of the environment, respectively. In what follows we shall be considered with two specific cases of the flux-gradient relation(1) for Fisher and Burgers' problem. *A. The Fisher equation with nonlinear damping and finite transport memory:* We start with an expansion of J in Eq.(1) [25] upto first order in τ to obtain

$$\tau \frac{\partial J(x, t)}{\partial t} + J(x, t) = -D \frac{\partial u}{\partial x} \quad (3)$$

Here $u(x, t)$ represents the density function. Differentiating (3) with respect to x and differentiating (2) with respect to t and eliminating J from the resulting equations one has

$$\frac{\partial^2 u}{\partial t^2} + [\beta - kf'(u)] \frac{\partial u}{\partial t} = \beta kf(u) + w^2 \frac{\partial^2 u}{\partial x^2} \quad (4)$$

where we have used the following abbreviations

$$\beta = 1/\tau \quad \text{and} \quad w^2 = \beta D \quad (5)$$

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Eq.(4), a hyperbolic reaction - diffusion equation is a generalization of Fisher equation for finite memory transport and nonlinear damping. It reduces to standard Fisher equation for $\tau=0$. Over the years the equation has drawn wide interest in the context of traveling wave solutions in various problems [7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23]. For example, Gally and Raugel [8, 9] have studied the propagation of front solution without the nonlinear term $kf'(u)$. Horsthemke has discussed some related issues in the problem of transport-driven instabilities [16].

We now look for the traveling wave solutions of Eq.(4) of the form $u(x, t) = KU(x-ct) \equiv KU(z)$ with $z = x-ct$, where $c > 0$ is the speed of the nonlinear wave (which, in general, is different from the linear wave w dictated by the medium subject to the boundary condition:

$$U(-\infty) = 1 \quad \text{and} \quad U(+\infty) = 0 . \quad (6)$$

Eq.(4) therefore after some algebra assumes the following form

$$\begin{aligned} \frac{\partial^2 U}{\partial z^2} + [c(n-A)] \frac{\partial U}{\partial z} - 2AcU \frac{\partial U}{\partial z} \\ + nAmU(1-U) = 0 = L(U) \quad (\text{say}) \end{aligned} \quad (7)$$

where

$$m = w^2 - c^2 \quad \text{and} \quad n = \beta/m \quad \text{and} \quad A = k/m \quad (8)$$

Following Murray [4] we now introduce the ansatz,

$$U(z) = \frac{1}{[1 + a \exp(bz)]^s} \quad (9)$$

as a solution to Eq.(7), where a , b and s are positive constants to be determined. Using (9) in (7) we obtain after some algebra

$$\begin{aligned} [s(s+1)a^2b^2 + nAma^2 - s[c(n-A)]a^2b \\ - sa^2b^2]e^{2bz} + [2aAmn - sab^2 - s[c(n-A)]ab]e^{bz} \\ + nAm - 2Ac s a b e^{bz}(1 + a e^{bz})^{-s+1} \\ - nAm(1 + a e^{bz})^{-s+2} = 0 = L(U) . \end{aligned} \quad (10)$$

Now for $L(U) = 0$ for all z , the coefficients of e^0 , e^{bz} , e^{2bz} and e^{3bz} within the curly brackets must vanish identically. This implies that $s=0, 1$ or 2 . $s=0$ is not a possible solution since s is a positive constant by our starting assumption. For $s=1$ the coefficients of e^{bz} and e^{2bz} of Eq.(10) yield the following relations,

$$s(s+1)b^2 + nAm - s[c(n-A)]b - sb^2 = 0 \quad (11)$$

$$nAm - sb^2 - s[c(n-A)]b - 2Ac s b = 0 \quad (12)$$

which can be solved to give $b=0$ and $b = -2Acs/(s+1)$.

Again since by initial assumption b is a positive constant, both the values of b are unacceptable and $s=1$ is not a correct choice.

For $s=2$ Eq.(10) reduces to a form in which the coefficient of e^{bz} , e^{2bz} and e^{3bz} must satisfy the following relations

$$s(s+1)b^2 + 3nAm - 2s[c(n-A)]b - 2sb^2 = 0 , \quad (13)$$

$$s(s+1)b^2 + nAm - s[c(n-A)]b - sb^2 = 0 \quad \text{and} \quad (14)$$

$$2nAm - sb^2 - s[c(n-A)]b - 2Ac s b = 0 . \quad (15)$$

From Eq.(13)-(15) we obtain

$$b^2 = nAm/[s(s+1)] \quad (16)$$

and putting $n = \beta/m$, $A = k/m$ from (8) and $s=2$ in (16) we have

$$b^2 = \beta k/(6m) . \quad (17)$$

Making use of (17) in (14) we obtain b in terms of c as follows.

$$c = 5k\beta/[6b(\beta-k)] \quad (18)$$

$$b = 5/\left[6c\left(\frac{1}{k} - \frac{1}{\beta}\right)\right] \quad (19)$$

The exact speed c of the traveling wave can be calculated from (17) and (19) using $m = w^2 - c^2$ as

$$c = \frac{\sqrt{\beta D}}{\left[1 + \frac{6}{25}(y - 1/y)^2\right]^{1/2}} \quad (20)$$

with $y = \sqrt{\frac{\beta}{k}}$. It may be noted that the exact value of c thus derived is always greater than c_{min} where

$$c_{min} = \frac{w}{\left[1 + \frac{1}{4}(y - 1/y)^2\right]^{1/2}} . \quad (21)$$

Again in the diffusive limit, i.e., $1/\beta \rightarrow 0$ or $1/y \rightarrow 0$ the expression (20) results in exact Fisher value of c as $c = 5\sqrt{kD}/\sqrt{6}$. It is necessary to stress that this is not the speed selected by the front ($c = 2\sqrt{kD}$), but it yields $2.04\sqrt{kD}$ which is very close to the selected value [4].

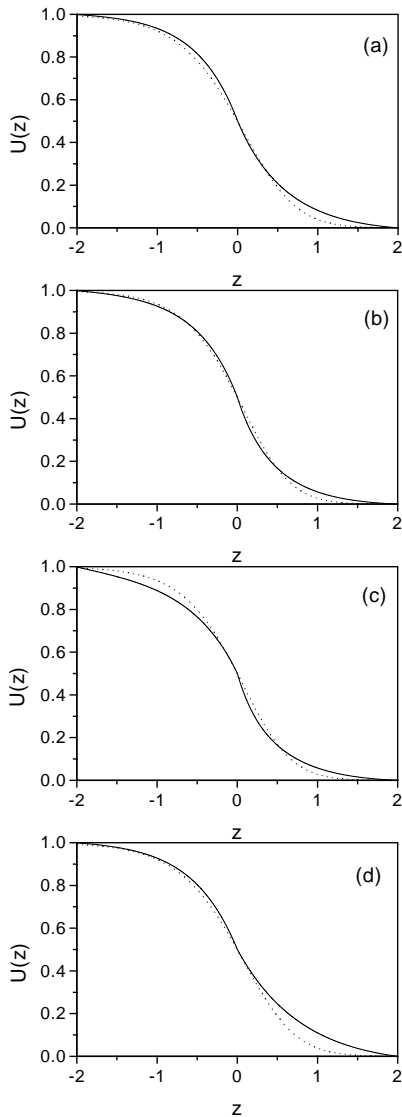


FIG. 1: A plot of travelling wave solutions for different values of relaxation time $\tau (= \frac{1}{\beta})$ for $k = 0.6$ and $D = 1.0$. The solid lines are due to numerical simulation of Eq.(4) and the dotted lines are the analytic results (22). (a) $\tau = 0.2$, (b) $\tau = 0.4$ (c) $\tau = 0.6$ and (d) $\tau = 0.0$ (Units are arbitrary).

Having determined b and s one can write down the exact form of the traveling wave solution (9) for the problem

$$U(z) = 1 / \left\{ 1 + a \exp \left[\left(\frac{5}{c\sqrt{6}(\frac{1}{k} - \frac{1}{\beta})} \right) \frac{z}{\sqrt{6}} \right] \right\}^2. \quad (22)$$

Furthermore a can be determined from the usual condition $U(z) = 1/2$ for $z = 0$. This results in $a = (\sqrt{2} - 1)$. The exact solution of the Fisher equation can be recovered from (22) in the limit $1/\beta \rightarrow 0$ (i.e., $1/y \rightarrow 0$) using

Fisher value of $c = 5\sqrt{kD}/\sqrt{6}$. This is given by

$$U(z) = \frac{1}{\left[1 + (\sqrt{2} - 1) \exp \left(\sqrt{\frac{k}{D}} \frac{z}{\sqrt{6}} \right) \right]^2}. \quad (23)$$

We thus observe that the effect of memory or finite relaxation time enters into the dynamics of the reaction-diffusion system through its influence on the speed of the traveling wave front c . We emphasize here that for $\frac{1}{\beta} = 0$ Eq.(22) does not give the solution selected by the front but is much steeper although the speed is very close to the selected one.

It is pertinent to point out that although exact the travelling wave solution (22) does not exhaust the possibility of other solutions. This was noted earlier by Murray [4] in the context of fisher equation without memory effect which is a parabolic differential equation. For an understanding of the nature of the travelling wave solution where $\beta = (1/\tau)$ is a new element of the present theory, we carry out a numerical investigation of Eq.(4) using finite difference method to solve the boundary value problem. The initial condition to integrate numerically is that the front is at rest at $t = 0$. We fix the value of diffusion coefficient $D = 1.0$ for the entire treatment. In order to allow the variation of τ for a fixed value of k , we have kept k at 0.6. For a higher value of k , i.e., where the reaction term dominates τ must be chosen appropriately over a range to generate numerically stable travelling wave front solution. The interplay of β and k will be considered in more detail in the later part of this section.

In Fig.1 we compare the analytical (dotted) and the numerical (solid) solutions corresponding to (22) and (4), respectively for different values of τ . From our analysis it is apparent that they agree fairly well for τ roughly in the range between 0.1 and 0.5. In Fig.1(d) we present the result for $\tau = 0$, which corresponds to the typical Fisher case. The analytical curve is marginally steeper than numerical one. In Fig.2 we compare the speed of the travelling wave front computed numerically from (4) with that obtained analytically following (20) for several values of τ . It follows that they agree reasonably well when $\tau \leq k$, i.e., in the range 0.1-0.5. As τ approaches zero the analytical value of c becomes lower than the numerical one. This implies that the analytical wave front although moves slower is steeper than the numerical one since steepness goes as $\sim \frac{k}{c}$ as noted by Murray in his earlier analysis. For higher values of τ the disagreement between analytical and numerical values of c grows rapidly.

The above analysis suggests that there is a strong interplay of k and τ (or β) in the dynamics so far as the form and stability of the travelling wave front solution is concerned. To explore this aspect more clearly we now carry out an asymptotic analysis of the problem. To this end we return to Eq.(7) subject to boundary condition (6). Following Murray we choose the perturbation

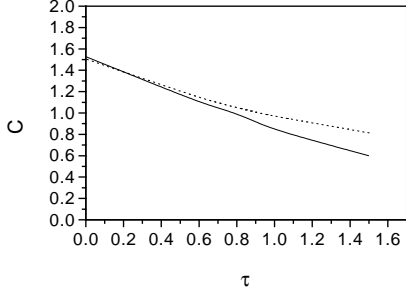


FIG. 2: A plot of the speed c of the travelling wave front solution vs relaxation time τ (analytical, dotted line; numerical, solid line) for $D = 1.0$, $k = 0.6$ (Units are arbitrary).

parameter $\epsilon = 1/c^2$ and look for the asymptotic solution for $0 < \epsilon \ll 1$ by introducing a change of variable $\xi = \frac{z}{c} = \epsilon^{1/2}z$ and $U(z) = g(\xi)$. With these transformations Eq.(7) and (6) therefore reduces to

$$\epsilon \frac{d^2 g}{d\xi^2} + (n - A + 2Ag) \frac{dg}{d\xi} + mnAg(1 - g) = 0 \quad (24)$$

and

$$g(-\infty) = 1 \quad ; \quad g(+\infty) = 0 \quad (25)$$

respectively. ϵ in the highest derivative in Eq.(24) identifies it as a singular perturbation problem.

Making use of a regular perturbation series in ϵ

$$g(\xi; \epsilon) = g_0(\xi) + \epsilon g_1(\xi) + \dots \quad (26)$$

in (24) we obtain after equating the appropriate powers of ϵ

$$(n - A + 2Ag_0) \frac{dg_0}{d\xi} = -mnAg_0(1 - g_0) \quad ; O(1) \quad (27)$$

and

$$(n - A + 2Ag_0) \frac{dg_1}{d\xi} + \frac{d^2 g_0}{d\xi^2} + 2Ag_1 \frac{dg_0}{d\xi} + mnAg_1(1 - 2g_0) = 0; O(\epsilon) \quad (28)$$

The lowest order equation (27) when integrated yields

$$\ln \left\{ \frac{(g_0)^{\beta-k}}{(1 - g_0)^{\beta+k}} \right\} = -\beta k \xi + \beta k l \quad (29)$$

where l is a constant of integration. Since we are interested in the solution in the vicinity of $z = 0$, i.e, $\xi = 0$ for which we put $g_0(\xi) = 1/2$, we obtain

$$l = \frac{1}{\beta k} \ln \left\{ \frac{(\frac{1}{2})^{\beta-k}}{(\frac{1}{2})^{\beta+k}} \right\} \quad (30)$$

Eq.(29) precludes the possibility of an explicit solution for $g_0(\xi)$. Depending on β and k we therefore consider three different cases;

(i) $\beta \gg k$ (or $\tau \ll k$): We have from (30) $l = 0$ and (29) reduces to

$$g_0(\xi) = (1 + \exp(k\xi))^{-1} \quad \text{or,} \quad U(z) = (1 + \exp(kz/c))^{-1} + O(\epsilon) \quad (31)$$

This is the standard asymptotic solution for $U(z)$ for which the effect of memory is negligible.

(ii) $\beta \approx k$ (i.e $\tau \approx k$): We obtain similarly from (29) and (30)

$$g_0(\xi) = \left(1 - \frac{\exp(k\xi/2)}{2} \right) \quad \text{or,} \quad U(z) = \left(1 - \frac{\exp((kz)/(2c))}{2} \right) + O(\epsilon) \quad (32)$$

When both β and k are small compared to 1 and the exponential term in (32) is small it is easy to put approximately the $O(1)$ term in the form of (31) as

$$U(z) \approx \left(1 + \frac{\exp((kz)/(2c))}{2} \right)^{-1} \quad (33)$$

(iii) $\beta \ll k$ (i.e $\tau \gg k$): We obtain

$$g_0(\xi) = \frac{1 \pm \sqrt{1 - \exp(\beta\xi)}}{2} + O(\epsilon) \quad (34)$$

The form of this solution is generically different from those of (32) and (31) since it is independent of k .

The three cases discussed above clearly shows that monotonic solutions satisfying $U(-\infty) = 1$ and $U(\infty) = 0$ for finite wave speed ($c \geq c_{min}$) exist for the cases (i) and (ii), i.e, when τ is short but finite; $\tau \leq k$. The assertion of this asymptotic analysis is in clear agreement with our numerical simulation and our choice of a smaller value of k as discussed earlier.

The aforesaid analysis clearly demonstrates that although the nature of the partial differential equation changes from parabolic to hyperbolic type due to the inclusion of relaxation time, the Fisher equation can be solved by Murray's ansatz [4] to derive the exact wave speed and the traveling wave front solution for a suitable range of relaxation time τ allowed by the strength of the reaction term. A compromise between the exact and the numerical solution can be obtained for relatively small reaction terms. The method can be extended further to study other density dependent diffusive processes.

Burgers' equation with finite memory transport: The Burgers' equation [6] is a simple model of turbulence which illustrates an interaction between convection and diffusion. The convection incorporates nonlinearity in

the dynamics. To include finite memory effect we proceed as follows:

We start with the following functional relation between flux $J(x, t + \tau)$ at a time $t + \tau$ and the field variable $u(x, t)$ and its gradient term at an earlier time t ;

$$J(x, t + \tau) = \frac{1}{2}u^2(x, t) - \gamma \frac{\partial u(x, t)}{\partial x} \quad (35)$$

where γ is a constant. Expanding J again upto first order in τ and differentiating the resulting equation with respect to x followed by differentiation of Eq.(2) for $k = 0$ (i.e., in the absence of any source term) with respect to time t and elimination of J as done in the last section we obtain

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} - \tau \frac{\partial^2 u}{\partial t^2} = \gamma \frac{\partial^2 u}{\partial x^2} \quad (36)$$

For $\tau = 0$ Eq.(36) assumes the form of classical Burgers' equation [1, 6] when $u(x, t)$ and γ are identified as the velocity field and kinematic viscosity, respectively.

We now seek a traveling wave solution of the Burgers' equation with memory (36) in the form, $U(z) = u(x - ct)$, $z = x - ct$, where c is again the wave speed to be determined. This results in the following equation:

$$-\left(\frac{c^2}{\beta} + \gamma\right) \frac{\partial^2 U}{\partial z^2} + U \frac{\partial U}{\partial z} - c \frac{\partial U}{\partial z} = 0 \quad (37)$$

where $\beta = 1/\tau$.

We now impose the bound condition on $U(z)$ that it asymptotically tends to constant values u_1 as $z \rightarrow -\infty$ and u_2 as $z \rightarrow +\infty$ and $u_1 > u_2$.

A direct integration of (37) yields

$$\frac{\partial U}{\partial z} = \frac{1}{2(\frac{c^2}{\beta} + \gamma)} (U^2 - 2cU - 2A) \quad (38)$$

where A is the integration constant. If u_1 and u_2 are the roots of the quadratic equation $U^2 - 2cU - 2A = 0$, then the wave speed c and the constant A can be obtained as

$$c = \frac{u_1 + u_2}{2} \quad \text{and} \quad A = -\frac{1}{2}u_1 u_2 \quad (39)$$

Eq.(38) can then be rewritten in the form

$$2\left(\frac{c^2}{\beta} + \gamma\right) \frac{\partial U}{\partial z} = (U - u_1)(U - u_2) \quad (40)$$

to integrate to obtain finally

$$U(z) = \frac{1}{2}(u_1 + u_2) - \frac{1}{2}(u_1 - u_2) \tanh \left[\frac{z}{4\delta} \right] \quad (41)$$

where δ is given by

$$\delta = \left(\frac{\frac{c^2}{\beta} + \gamma}{u_1 - u_2} \right) \quad (42)$$

The above analysis shows that the shape of the wave form is not only affected by kinematic viscosity γ by also by an additional contribution c^2/β due to finite relaxation time $\tau (= 1/\beta)$ such that $(c^2/\beta) + \gamma$ behaves as effective kinematic viscosity. It is thus apparent that the balance between the steepening effect of the convection as well as smoothening effect due to kinematic viscosity is enhanced by the presence of the wave speed dependent term c^2/β . Thus although wave speed $c[(u_1 + u_2)/2]$ itself remain unaffected by the finite memory effect in contrast to our earlier case of Fisher equation, transmission layer thickness ' δ ' - which is a measure of shock thickness, increases for higher speed c and relaxation time τ . This implies that as the wave moves faster the shock smoothenes out more and more so that the speed dependence of thickness δ makes the dynamics self-regulating in the problem of interaction between convection and diffusion.

Conclusions: The existence of relaxation or delay time is an important feature in reaction-diffusion and convection-diffusion systems. In this paper we have shown that two prototypical representatives of these systems a generalized Fisher equation and Burgers' equation can be solved exactly for finite arbitrary delay time using conventional methods. While the wave speed is significantly modified in the Fisher problem for finite memory transport, speed of the traveling wave in the corresponding Burgers' problem remains unaffected, delay time being effective in smoothening out the shock-wave nature of the traveling wave. We also establish numerically that for the reaction-diffusion system the strength of the reaction term must not exceed a critical limit to allow travelling wave front solutions to exist for appreciable memory or relaxation effect. In view of the fact that the studies on reaction-diffusion and convection-diffusion with finite memory transport have been applied to forest fire [21] and population growth models [14], Neolithic transitions [22] and in several other areas under various approximate schemes [10, 11, 12, 13, 15, 16, 17, 18, 19, 20], we believe that the present exact solutions for the generalized Fisher and Burgers' problem are very much pertinent in this context.

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- [1] L. Debnath, *Nonlinear Partial Differential Equations for Scientists and Engineers* (Birkhäuser, Boston, 1997).
 - [2] I.R. Epstein and J.A. Pojman, *An Introduction to Nonlinear Chemical Dynamics: Oscillations, Waves, Patterns and Chaos* (Oxford, New York, 1998).
 - [3] N.F. Britton, *Reaction-Diffusion Equations and their applications to Biology* (Academic, New York, 1986).
 - [4] J.D. Murray, *Mathematical Biology*, Second, Corrected Edition (Springer, Berlin, 1993).
 - [5] R.A. Fisher, *Ann. Eugenics* **7**, 353 (1937).
 - [6] J.M. Burgers, *Adv. Appl. Mech.* **1**, 171 (1948).
 - [7] J. Fort and V. Méndez, *Rep. Prog. Phys.* **65**, 895 (2002).
 - [8] Th. Gallay and G. Raugel, *ZAMP* **48**, 451 (1997).
 - [9] Th. Gallay and G. Raugel, Preprint patt-sol/9809007; Preprint patt-sol/9812007 .
 - [10] E.E. Holmes, *Am. Nat.* **142**, 779 (1993).
 - [11] K.P. Hadeler, *Can. Appl. Math. Quart.* **2**, 27 (1994).
 - [12] K.P. Hadeler, in *Reaction Transport Systems in Mathematics Inspired by Biology*, edited by V. Capasso and O. Diekmann, CIME Lectures, Florence (Springer-Verlag, Berlin, 1998).
 - [13] T. Hillen, *Math. Models Methods Appl. Sci.* **8**, 507 (1998).
 - [14] V. Méndez and J. Camacho, *Phys. Rev. E* **55**, 6476 (1997).
 - [15] W. Horsthemke, *Phys. Lett. A* **263**, 285 (1999).
 - [16] W. Horsthemke, *Phys. Rev. E* **60**, 2651 (1999).
 - [17] K.K. Manne, A.J. Hurd and V.M. Kenkre, *Phys. Rev. E* **61**, 4177 (2000).
 - [18] G. Abramson, A.R. Bishop and V.M. Kenkre, *Phys. Rev. E* **64**, 066615 (2001).
 - [19] S. Fedotov, *Phys. Rev. Lett.* **86**, 926 (2001).
 - [20] J.M. Sancho and A. Sánchez, *Phys. Rev. E* **63**, 056608 (2001).
 - [21] V. Méndez and J.E. Llebot, *Phys. Rev. E* **56**, 6557 (1997).
 - [22] J. Fort and V. Méndez, *Phys. Rev. Lett.* **82**, 867 (1999).
 - [23] S. Kar, S.K. Banik and D.S. Ray, *Phys. Rev. E* **65**, 061909 (2002).
 - [24] C. Cattaneo, *C. R. Acad. Sci.* **247**, 431 (1958).
 - [25] M. Kot, *Elements of Mathematical Ecology* (Cambridge University Press, Cambridge, 2001).